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# EVOLUTION AND DEVELOPMENT OF BRAIN ASYMMETRY, AND ITS RELEVANCE TO LANGUAGE, TOOL USE AND CONSCIOUSNESS

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A brain is said to be asymmetrical or lateralised if one hemisphere is structurally different from the other, or if each hemisphere controls a different set of functions. If the majority of individuals in a population have asymmetries of the same kind and in the same lateral direction, we say that there is hemispheric specialisation. For a long time Western science argued that lateralisation or hemispheric specialisation was a unique characteristic of humans, explaining our "superior" abilities in tool use and language (reviewed by Bradshaw & Rogers, 1992). Indeed, there are still some who essentially adhere to this notion at the present time, seeing cerebral asymmetry as unique to humans at least in its extent, pattern and bias within the population (Corballis, 1991). Brain lateralisation has also been considered as providing a possible basis of consciousness (Eccles, 1989; and reviewed by Rogers, 1995a). Furthermore, group differences in brain asymmetry have been variously used in attempts to provide biological explanations for sex differences in behaviour (see below), schizophrenia (Gruzelier & Floor-Henry, 1979; Nasrallah, 1982), stuttering, dyslexia (Dunlop & Dunlop, 1974), alcoholism (Nasrallah, Keelor & McCalley-Whitters, 1983; Ellis & Oscar-Berman, 1989) and, as a current fashion, sexual orientation (Geschwind & Gallaburda, 1987; McCormick, Witelson & Kingstone, 1990; Dellatolas, Annesi, Jallon, Chavance, & Lellouch, 1990). In every case, the behaviour in question is tied to a difference in brain asymmetry said to be caused biologically by the action of genes or hormones on the

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brain. These simplistic explanations need much closer scrutiny.

One of the earliest theories linking brain asymmetry to sex differences in behaviour suggested that, because women are more emotional than men, they must be more right-hemisphere dominant (reviewed by Star, 1979). This theory ignored the fact that women have superior verbal ability, and that this function is located in the left hemisphere. Another hypothesis, known as the Levy-Sperry hypothesis, argued that women have *less* lateralised brains than men, whereas yet another (proposed by Buffery & Gray, 1972) claimed that women have *more* lateralised brains. The latter two hypotheses were based on *ad hoc* deductions made about sex differences in performance of spatial tasks (for more detail see Star, 1979; Rogers, 1988).

Similarly, in the case of schizophrenia some claim that there is impaired functioning of the right hemisphere (Bellini, Gambini, Palladin, & Scarone, 1988). Others suggest that the impairment is in the left hemisphere (Gur, 1978; Nasrallah, 1982), thus causing more dependence on the right, "dark" or sinister hemisphere. Attempts have also been made to link schizophrenia, as well as a number of other neurological conditions, to disturbed asymmetries in neurotransmitter levels (Glick, Ross & Hough, 1982), but again there is no conclusive evidence on this matter.

In all of the other behavioural conditions to which brain asymmetry has been applied, there are similar contradictory views, and a lack of convincing evidence. Brain asymmetry is thus a scientific concept with broad ramifications into social attitudes.

The presence of asymmetry in the human brain has been recognised for more than a hundred years. In 1836 Dax noticed that patients suffering from disturbances of speech had damage to the left hemisphere, and not the right. Soon after, Broca associated right side paralysis with aphasia, the inability to produce speech, and located the damage to a region in the left hemisphere now known as Broca's area. In 1874 Wernicke found that damage to another region in the left hemisphere, now called Wernicke's area, caused loss of language understanding while not affecting speech production. Today we can visualise activity in these brain regions using computer imaging techniques, which allow determination of regional activity in the living brain as it performs certain functions. Positron emission tomography, for example, allows imaging of changes in blood flow as a person hears, sees, speaks or generates words. Each of these processes leads to increased blood flow, and nerve cell activity, in different regions of the left hemisphere. Incidentally, the same regions of the left hemisphere are specialised for both spoken and signed language in humans (Bellugi,

Poizner & Klima, 1989).

Other forms of neural processing, such as listening to chords and tones without analysing them, increases activity predominantly in the right hemisphere. When the subject analyses the chord structure, left hemisphere activity is greater (Peretz & Morais, 1988). Broadly speaking, the left hemisphere is used for analytical, sequential thinking, whereas the right is used for parallel, or holistic, thinking. It must be emphasised nevertheless, that the left-right dichotomy is not absolute, and varies amongst individuals, partly depending on past experience, and between tasks (Kinsbourne, 1978).

In the human brain this division of function between the hemispheres is manifest in structural asymmetries and in lateralised motor behaviours. Each hemisphere controls the opposite side of the body, including the muscles of the face. Thus, the fact that emotions are expressed more strongly on the left side of the face (Christman & Hackworth, 1993) reflects control by the right hemisphere. We also pay greater attention to expressions on the left side of another person's face or a photograph of a face. By contrast, during speech, which is under left hemisphere control, the right side of the mouth moves more than the left (Wolf & Goodale, 1987).

Gross anatomical asymmetry of the brain is visible even to the naked eye. The left hemisphere is wider in the posterior region, where visual inputs are processed, and the right is wider in the anterior region. This skewed anatomy of the brain impresses itself on the interior side of the skull, and so can be seen in endocasts of the skulls of fossil hominids. They too had asymmetrical brains.

Other evidence indicates that the hominids were right handed. For example, the fracture patterns of prehistoric stone tools indicate that the tool being made was rotated clockwise, suggesting that it was held in the left hand while being struck with a hammer stone held in the right hand, just as a right-handed person would today (Toth, 1985). From this and other evidence for right handedness in early humans, together with the predominance of stone axes that can be most effectively used by the right hand, anthropologists have drawn an association between the evolution of tool use and language ability (Bradshaw & Rogers, 1992). Neurobiologists have added the third side to the triangle, by including brain asymmetry as the basis for both behaviours.

As all of these attributes (brain asymmetry, tool use and language) were considered to be unique to the human species, a conceptual divide had been constructed between humans and other animals. Those who adhered to this view were saying in essence that, although we evolved from monkeys and apes, we made a huge evolutionary leap away from

them. But, there is now overwhelming evidence that asymmetry of brain function occurs in a wide number of species, and that lateralised biases in behaviour may have evolved at least as early as fish. For example, Reist, Bodaly, Fudge, Cash, & Stevens (1987) have reported that whitefish, *Coregonus sp.*, have more superficial scars on the left side of the body. These scars are attributed to lampreys and the lateral bias suggests that the whitefish is better able to remove lampreys from its right side by rubbing them against surfaces or that the lampreys have a lateral bias that leads them to attach to the left side of the whitefish more readily. This population bias might possibly reflect a bias for turning or a side preference. There is other evidence for a turning bias in fish; *Girardinus falcatus* exhibits a significant population bias to turn right when first presented with the shape of a simulated predator and to the left on subsequent presentations (Cantalupo, Bisazza, & Vallortigara, 1994). The early evolution of lateralisation of brain function is also supported by a report of lateralised neural control in an amphibian: the frog, *Rana pipiens*, controls its alarm vocalisation by the left side of the brain (Bauer, 1993). Examples of lateral biases in other species are discussed below, but for a more comprehensive summary see Bradshaw and Rogers (1992).

For tool use too, humans are not unique. There is a growing list of examples of tool use by animals. Chimpanzees use sticks to "fish" termites from their nest (McGrew & Marchant, 1992), and rocks to crack open nuts placed on a tree root or another rock as an anvil (Boesch, & Boesch, 1982). Moreover, the chimps appear to *be aware of* the function of the stones as tools because they immediately place the nut on the hardest spot of the anvil (Sakura, & Matsuzawa, 1991). Sea otters too use a rock as a hammer to crack open shell fish (Kenyon, 1969), and some species of finches on the Galapagos Islands use cactus spines to probe into crevices and impale insects (Millikan & Bowman, 1967). Elephants have been reported to perform 21 types of tool use, with 22 acts per hour in captive animals and half as often in wild ones (Chevalier-Skolnikoff, & Liska, 1993). The latter authors conclude that tool use is so common that, of course, not only did it appear well before humans evolved, but it may well have originated a number of times in different phylogenetic groups, each time for a different purpose.

To fashion a tool for a particular use is considered to require a higher cognitive ability. The chimpanzees carefully select the sticks that they use for termite fishing and they break them to the desired length (McGrew & Marchant, 1992). Wild orang-utans similarly probe holes with sticks that they fashion so that they have a spatulate form at one end, to be held firmly in the mouth, and are chewed at the other end, to



be inserted in the hole possibly to soak up honey (van Schaik & Fox, 1994).

There are many other examples of tool use in wild and captive primates (Bard, 1990; Brewer & McGrew, 1990; Galdikas, 1982; Rogers & Kaplan, 1994; Visalberghi, 1987), but few studies have consistently reported whether the tool use involves handedness, as in humans. Westergaard (1991) has reported left handedness in capuchins, *Cebus apella*, and lion-tailed macaques, *Macaca silenus*, for holding and manipulating dipping sticks. McGrew and Marchant (1994) have reported a weak, but significant, bias for left handedness in wild chimpanzees performing termite fishing. For holding the hammer when cracking nuts, chimpanzees display individual hand preferences but there appears to be no consistent handedness in the population (Boesch, 1991; Sugiyama, Fushimi, Sakura, & Matsuzawa, 1993). There is a need to collect more information on hand preferences in tool use, and it is premature to conclude that, unlike humans, nonhuman primates do not have strong handedness for tool use.

Contrary to earlier indications, there is now ample evidence that many primate species exhibit handedness for picking up and holding food (reviewed by Bradshaw & Rogers, 1995; Ward & Hopkins, 1993). Early investigations of hand preferences in primates seemed to show that there were hand preferences at an individual level but no predominant bias for use of the same hand (i.e. handedness). These reports, however, were dogged by small sample sizes and poor data sampling, and a reanalysis of the original findings has indicated the presence of handedness (MacNeilage, Studdert-Kennedy & Lindblom, 1987). For instance, the lower primates, prosimians, are left handed for holding food (reviewed by Ward, & Hopkins, 1993). The right hand may have a stronger grip and thus it may be used for holding on to the tree branches. According to MacNeilage et al. (1987), as primates evolved to being less arboreal, the right hand was freed for use in manipulating, and a shift to right handedness for fine motor acts could occur. Such right-hand preferences have been reported in some studies of chimpanzees (Bard, Hopkins, & Fort, 1990 ; Hopkins & Bard, 1993; Hopkins, Bard, Jones, & Bales, 1993) and gorillas (Olson, Ellis, & Nadler, 1990). In orang-utans, there is no predominant handedness for food holding and manipulation in the population as a whole, possibly because orang-utans are arboreal, although older females are more likely to be right-handed (Rogers & Kaplan, 1995) and this is inconsistent with the hypothesis of MacNeilage et al. (1987), which predicts left handedness in arboreal species. In fact, apparently like humans, orang-utans have a preference for touching the face with the left hand, in their

case when they manipulate parts of the face as in cleaning the teeth, eyes or nose (Kaplan & Rogers, 1994; Rogers & Kaplan, 1995).

The other branch of the primate evolutionary tree, that of the New World monkeys, has been less well studied for handedness. Most emphasis has been on hand preferences in the common marmoset, *Callithrix jacchus*. For holding food, individuals of this species are either left or right hand preferent or have no hand preference but there are more left-hand preferent individuals, even though this bias towards left handedness is not strong (Box, 1977; Hook-Costigan & Rogers, 1995). This species appears never to have evolved, or possibly to have lost, a strong bias for handedness within the population, but nevertheless individuals retain hand preferences, and thus lateralised brains.

It should be mentioned here that, although preferred use of a particular hand reflects lateralisation of the brain, it does not in itself indicate how that lateralisation is determined. It may have come about by the process of evolution, as suggested for populations in which there is a consistent preference for all or most individuals to use the same hand to perform similar functions, or the preference may be learned and thus the learning establishes brain lateralisation.

In contrast to their weak lateralisation for handedness, marmosets have a strong population bias for processing certain forms of visual information: they prefer to use the right eye for peeping through a hole to view food and a range of other stimuli (Hook-Costigan & Rogers, 1995). "Eyedness" has also been shown in a lower primate species, *Otolemur garnettii*, but in this case the preferred eye for viewing food is the left eye (Rogers & Ward, 1994). There is evidence to suggest that these eye preferences reflect perceptual rather than motor lateralisation (Rogers & Ward, 1994) and, therefore, marmosets may have retained lateralisation for perceptual processing but not motor performance. The eye preferred for viewing depends on the stimulus being viewed and the state of arousal of the subject (Rogers & Ward, 1994). These variables have not been considered in studies of humans that have used shifts of eye dominance from the right to the left eye as indicators of neurochemical imbalances underlying, for example, schizophrenia and alcoholism (see above).

Other New World primates do, however, display handedness. As mentioned above, capuchins are left handed for holding dipping sticks and squirrel monkeys, *Saimiri sciureus*, are right-hand and right-foot preferent for scratching and touching their bodies (Aruguete, Ely, & King, 1992), to give just two examples.

Thus, nonhuman primates display lateral biases on a range of behaviours, but some of the best examples of lateralisation are for birds.

Knowledge of "footedness" in parrots (most prefer to hold food objects in the left foot) has a history three centuries long (Harris, 1989), but this was ignored until recently. Now it is recognised that parrots exhibit strong footedness equivalent to that of handedness in humans (Rogers, 1980; reviewed by Bradshaw & Rogers, 1992).

In the early 1970s Nottebohm (1971) demonstrated that many species of songbirds, such as the chaffinch and canary, have brain asymmetry for control of singing by the left hemisphere only. Many songbirds have individually characteristic songs, which can be analysed in a linguistic framework to contain elements, syllables and phrases. The song is produced by the syrinx in the trachea, and each side of the syrinx is controlled by a branch of the hypoglossal nerve from the ipsilateral side of the brain. Sectioning the right nerve has no effect on an individual's ability to sing, but sectioning the left nerve mutes the bird. Nottebohm described the latter birds as performing like actors in a silent film. They stood on the perch performing all of the beak, wing and body movements used in singing but uttered no more than an occasional click or a short phrase. A similar loss of song was obtained if the higher vocal centre in the left hemisphere was lesioned, but not if the same region in the right hemisphere was lesioned. This was the first clear example of brain asymmetry being present in a nonhuman animal.

Evidence for asymmetry of brain function in the chicken first became available in the late 1970s (Rogers & Anson, 1979). When a hungry chick searches for grains of food scattered on a background of small pebbles, it will soon learn to discriminate between the two stimuli if it is tested binocularly or monocularly with the right eye open, but when it is tested monocularly with the left eye open it takes much longer to find the food and often gives up the search altogether (Mench & Andrew, 1986; Zappia & Rogers, 1987). As each eye sends its visual information to the thalamus and optic tectum on the contralateral side of the brain and from there most projections go to the forebrain hemisphere on the same side, it is the left hemisphere which is able to categorise food from "nonfood". Recently, it has been shown that the left-hemisphere of the chick is also used to categorise other stimulus types, including members of the same species (Rogers, 1995b; Vallortigara & Andrew, 1991, 1994). The left eye and right hemisphere, by contrast, attends to the details of each individual stimulus. For example, when given a choice between a familiar cage-mate and a strange chick, chicks tested monocularly using the left eye discriminate between the companion and the stranger, whereas those using the right eye discriminate less clearly or not at all (Vallortigara & Andrew, 1994). In other words, the left eye and right hemisphere recognises and responds

to chicks as individuals, rather than as a category, much as the right hemisphere of humans recognises faces. In fact, one cannot fail to be struck by the similar functions performed by each hemisphere in chicks and humans.

The left eye and right hemisphere also attend to the position of the stimulus in space. Thus, a chick using its left eye has better spatial learning ability than one using its right eye (Rashid & Andrew, 1989). A chick using the left eye is also more fearful (emotional) and shows elevated copulation levels following treatment with the male sex hormone testosterone. It is well-known that chicks tested binocularly following treatment with testosterone show elevated copulation at a precocious age, but remarkably those tested monocularly using the right eye behave as if they had never been treated with the hormone (Rogers, Zappia, & Bullock, 1985). Therefore, only those neural circuits connected to the left eye have access to the region of the brain which has a lowered threshold for copulation following the testosterone treatment.

A large amount of evidence for such asymmetries is now available for the chick. In fact, the chick, with its laterally placed eyes and very small area of binocular overlap in the visual field, is surrounded by two different visual worlds. It responds differently to stimuli perceived in its left or right monocular fields. Another chick might be less likely to be attacked if it approaches an aggressive chick on its left side.

Although the evolutionary significance of these asymmetries may lead some to believe that they are genetically determined, this is not so. Environmental factors have a crucial influence on various forms of brain asymmetry. For example, I have shown that the asymmetries in the visually guided behaviour of the chick are not solely the result of genetic determinants. During the last few days before hatching, the chick embryo is oriented in the egg so that its left eye is turned against its body and is therefore occluded, whereas the right eye is placed next to the air sac. Light entering the egg through the shell and membranes reaches the right eye at a stage when its visual connections to the forebrain are forming, and promotes growth of those visual pathways that are connected to the right eye (Rogers & Sink, 1988; reviewed in Rogers, 1995b). Thus, the lateralisation of various visual functions, although not all functions, may occur as a consequence of asymmetrical light stimulation from the environment (Rogers, 1982). The direction of the asymmetry can be reversed by pulling the embryo's head out of the egg before hatching, occluding the right eye and exposing the left eye to light. These chicks learn better when they use the left eye and right hemisphere, and they control attack and copulation with the left hemisphere (Rogers, 1990). Chicks hatched from eggs incubated in

darkness have no asymmetry for control of these behaviours.

These results show clearly that the asymmetry results from an interaction between genetic and environmental factors. We have shown that hormonal factors also have an influence (Rogers & Rajendra, 1993; Schwarz & Rogers, 1992). The light-dependent growth of the visual pathways connected to the right eye occurs only if there are low circulating levels of the sex hormones, testosterone and oestrogen, in the embryo. In fact, in male chick embryos the testes reduce their production of testosterone just at the time when the light stimulation has its effect.

The chick provides us with a model system which demonstrates that one cannot speak of unitary causes for brain asymmetry. The development of asymmetry is not determined just by the action of a hormone, the genes or environmental factors, but by all of these influences contributing in a completely integrated way. Therefore, popular attempts to explain sex differences in human behaviour simply in terms of the action of sex hormones on the development of brain asymmetry are inadequate (e.g. Geschwind & Galaburda, 1987). It is not possible to separate biological from environmental determinants (that is, genetic or hormonal influences from learning/social influences).

Learning itself can impose neurochemical asymmetries on the chicken brain. When a young chick imprints on or forms a strong attachment to an attractive stimulus, usually its mother but in the laboratory it can be a coloured box or the like, neurochemical changes occur in its left hemisphere as the memory is laid down (Johnston, Rogers, & Johnston, 1993; McCabe & Horn, 1988). Thus, the early learning experience imposes new asymmetries on the developing brain. Similar effects of early learning may effect brain asymmetry in humans.

Birds also have asymmetries for processing auditory information. In chicks the left hemisphere learns to ignore irrelevant auditory stimuli, to categorise them as uninteresting (Rogers & Anson, 1979). The perception of song involves lateralized processes but it is not limited to the left side of the brain. Unilateral lesions placed in the input side of the auditory system (in the left or right nucleus ovoidalis) affect song perception differentially. Following the placement of a lesion in the left nucleus ovoidalis a zebra finch is unable to discriminate between two familiar songs, an ability which the intact bird possesses. Following placement of the lesion in the right nucleus ovoidalis, the zebra finch retains its ability to distinguish two whole songs but has an impaired ability to detect a missing harmonic in a syllable of a song (Cynx, Williams, & Nottebohm, 1992). Thus, as Nottebohm et al. (1990) suggest, the left hemisphere of the zebra finch may be better at

discriminating between stimuli in a 'holistic' sense, whereas the right hemisphere is better at making discriminations which require analysis of components of the song.

What relevance do all these asymmetries in birds have to other species? Since birds diverged from the line to mammalian (and human) evolution at the level of a common reptilian ancestor, the evidence would point again to an early evolution of brain asymmetry. Mention has been made previously about lateralised motor responses in fish. Indeed, it is now known that some form of asymmetry existed at the time of the early trilobites. Fossils of trilobites have a higher incidence of predator-inflicted injuries on the right posterior region of their bodies (Babcock, & Robison, 1989), indicating that they were either more, or less, successful at escape when they moved leftwards, or that their predator had an asymmetry in its direction of attack. Thus, asymmetry of the brain must have evolved very early, soon after the brain structurally duplicated itself.

As we "ascend" the mammalian branch of the evolutionary tree, we find ample evidence for brain asymmetry in rodents (Denenberg, 1981). Although rats and mice show no population bias for right or left handedness (pawedness) when they are tested on a task which requires them to reach into a small tube for a food reward, other tests have shown clear lateralisation of brain function. The right hemisphere analyses spatial information and controls emotional behaviour. The left hemisphere is used for identifying species-specific vocalisations (Ehert, 1987) and for sequential analysis (Bianki, 1988). Rats using the left hemisphere perform better in conditioning situations when a series of stimuli are presented one after the other, and those using the right hemisphere perform better when the stimuli are presented simultaneously (Bianki, 1988). One notices the similarity to the division of function between the hemispheres of the human brain. Also, as shown in the chick, the asymmetry in rats depends on the interaction between sex hormone levels and environmental stimulation during neonatal life (Denenberg, Fitch, Schrott, Cowell, & Waters, 1991).

It is now obvious that brain asymmetry preceded human language and tool use. While it can still be argued that human language evolved as recently as 35,000 years ago (Davidson & Noble, 1989), it can no longer be accepted that it suddenly appeared without neural precursors in other species. Rather, the neural requirements of language and tool use formed over a long evolutionary trajectory (Bradshaw, & Rogers, 1992).

Furthermore, in primates, like humans, the left hemisphere processes the species-specific vocalisations (Petersen, *et al.* 1984). Specialisation

of the left hemisphere for processing species-specific vocalisations in rats, primates and humans may not be coincidental. Moreover, humans process certain language sounds, such as the voicing contrast 'ga' versus 'ka', in the right hemisphere and so too do dogs (Adams, Molfese & Betz, 1987). While primates, and dogs, do not have the vocal apparatus to produce human speech, it is possible that they analyse it much as humans do and that they understand it much better than we think. The ability to analyse language-like vocalisations may have preceded the ability to produce speech by a long period of evolution.

Present knowledge shows that there is a continuum from animals to humans on the attributes once thought to be uniquely human, and that simplistic explanations of human behaviour are not supported by the research on model systems in animals. It is inadequate to opt for biological determinism of complex behaviour, such as schizophrenia, alcoholism or gender differences in behaviour. Genes or hormones do not act alone as biological determinants, but rather they interact with environmental factors to produce the unique pattern of brain organisation within the individual. Furthermore, environmental influences may affect the organisation of the brain throughout the life span. Although exposure to certain forms of environmental stimulation and the formation of memories may have more profound effects during embryonic and neonatal life than in adulthood, older brains can also be modified by environmental stimulation. We now know that the brain is in dynamic interaction with its environment throughout life, and thus its pattern of asymmetry may shift in response to learning, stress factors or other forms of environmental input.

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## THE DISTANCE CALL OF DOMESTICATED ZEBRA FINCHES (*POEPHILA GUTTATA*)

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**ABSTRACT:** Wild zebra finches use distance calls in a wide variety of contexts including flight, mild alarm, perching, and courtship. The call is also thought to allow paired males and females to maintain contact in large flocks. The purpose of this study is to compare the acoustic structure of distance calls of wild and domesticated zebra finches. We analyzed distance calls from our own colony and combined the results of this analysis with the findings from two other published studies on distance calls of domesticated finches. The results from these studies were compared to earlier research on the distance calls of wild zebra finches.

Overall, domesticated male and female zebra finches produce calls that have longer duration, lower fundamental frequency, and higher frequency of maximum amplitude than those of wild zebra finches. These differences were generally consistent across different domesticated populations. Domesticated males produce distance calls in which the frequency modulation of the noise element is substantially different from the noise element of wild males. Furthermore, there was little consistency in the structure and location of the male's noise element across different domesticated populations. It remains to be demonstrated whether these changes have altered the function of this call in domesticated finches.

### INTRODUCTION

According to Immelmann (1965), zebra finches have three basic calls: the loud identity call, the low communication call, and an aggressive call. Unfortunately, different researchers have used different names to denote these calls. For example, the loud identity call has been referred to as the distance call (Zann, 1984, 1985), the lost call

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(Immelmann, 1965), the long call (Price, 1979; Simpson & Vicario, 1990), and the lure call (Lombardi & Curio, 1985). The low communication call has been referred to as the tack call (Lombardi & Curio, 1985), and the short call or medium call (Price, 1979). Although researchers have performed numerous studies on song and song development in zebra finches (See Slater et al., 1989 for a review), they have expressed nowhere near this level of interest in the zebra finch's calls. This is somewhat surprising since male finches incorporate a number of these calls into their song (Price, 1979; Zann, 1990).

The loud identity call, or distance call, is the only call that has been subjected to detailed analysis. Zann (1984, 1985) performed two studies on wild zebra finches in which he described the acoustic features of the distance call and examined the experiential factors that were important in its development. Okanoya et al. (1993) examined the acoustic properties of this call in three different populations of domesticated zebra finches. In addition, Okanoya and Dooling (1991 a, b) and Dooling et al. (1992) used distance calls to investigate species-typical auditory processes across a number of species. Finally, Simpson and Vicario (1990) used distance calls to examine the neural pathways that controlled the production of learned vocalizations. Interestingly, the function of this call has not been examined in an experimental setting.

The distance call is produced by both males and females in a wide variety of contexts including flight, mild alarm, perching, and courtship (Zann, 1984). The call is thought to allow paired males and females to maintain contact (Zann, 1984). Most males learn their distance calls from the distance calls and song of their father (Zann, 1990). Females, on the other hand, do not need to hear species-typical distance calls in order to develop normal distance calls themselves (Zann, 1985). Males incorporate the distance calls of their father and other males into their song. Those portions of song that resemble distance calls are referred to as distance call elements. A male may have distance call elements in his song that do not resemble his distance call, but that do, nonetheless, look like distance calls on a sound spectrogram (Zann, 1990).

Most researchers who study zebra finches use domesticated finches as subjects. Domestication has resulted in a number of behavioral, developmental, and morphological changes (Sossinka, 1982; Carr & Zann, 1986). Domesticated zebra finches from European collections tend to be larger, less active, exhibit a greater variety of color morphs, undergo slower gonadal maturation, and engage in lower levels of courtship than their wild counterparts. Slater and Clayton (1991) found a number of subtle differences between the song of wild and domesticated finches. They found that domesticated males were likely

to have faster song tempo, shorter phrase length, and fewer distance call elements in their song. In addition, Zann (1990) stated that the distance call element is absent or distorted beyond recognition in the song of domesticated zebra finches.

There is evidence that domesticated zebra finches also produce distance calls that are different from those of wild finches. Sound spectrograms of distance calls of domesticated finches reported by Price (1979), Okanoya and Dooling (1991 a, b), Dooling et al. (1992), Okanoya et al. (1993), and Simpson and Vicario (1990) are quite different from those of wild finches (Zann, 1984, 1985). Furthermore, there are also striking differences in the acoustic structure of distance calls of domesticated finches reported by these researchers.

Distance calls play an important role in the social interactions of wild male and female zebra finches. Before any studies on the function of this call among domesticated finches are undertaken, it is important to understand the extent to which distance calls of domesticated zebra finches differ from the calls of wild finches, and the extent to which such changes are consistent across domesticated populations. The purpose of this study was to compare the acoustic properties of distance calls of wild and domesticated zebra finches. To accomplish this we analysed distance calls from our population of domesticated finches and examined previous research on distance calls of domesticated finches by Okanoya et al. (1993) and Simpson and Vicario (1990). We compared these findings to Zann's (1984) work on distance calls of wild finches.

## METHOD

### *Subjects*

We used 26 adult domesticated zebra finches (15 males and 11 females) that were either purchased from local breeders or bred in our aviary (6.1 x 6.1 x 2.5 m). Normally, there were 25–30 birds in the aviary. They were fed and watered *ad libitum*. Their diet consisted of commercial finch food, grit, and vitamin supplements. Lights in the aviary were on a 14 h: 10 h light/dark cycle. The birds also received sunlight through a window near the side of the aviary. Thus, daylength varied throughout the year.

Okanoya et al. (1993) used two populations of domesticated finches. One population (ANR–American normal reared) was obtained from breeders in Maryland, and a second population (JNR–Japanese normal reared) was obtained from Japanese breeders. We did not include

Okanoya et al.'s findings on finches that were foster reared by Bengalese finches. Simpson and Vicario (1990) obtained their domesticated finches from a local supplier in New York or from their own breeding colony.

### *Recording Procedure*

We used the same procedure that Zann (1984, 1985) used to evoke and record distance calls from wild birds. We captured birds with either a mist net or a bait trap. They were banded and placed in a small (.35 x .35x .35 m) cage. The cage was removed from the aviary and placed behind a barrier approximately 2 m from the aviary. Thus, the bird in the cage could hear but not see the birds in the aviary. To reduce background noise, we placed the cage in a foam-lined enclosure (.75 x .5 x .64 m) that was open on the top and the side facing the aviary. An AKG C 568 EB directional microphone was placed approximately 5 cm from the cage. The microphone was connected to a Crown PH-1a phantom power supply which in turn was connected to a Marantz 221 PMD cassette recorder. After the cage was placed in the foam-lined enclosure, the cassette recorder was turned on, and all personnel left the room. One hour later, we returned and collected the tape. Only experimentally naive birds were recorded. Okanoya et al. (1993) and Simpson and Vicario (1990) used similar methods to record distance calls.

We reviewed the tape and located the distance calls. Distance calls are the loudest and longest calls that zebra finches produce in this context, and they are easily recognizable (Zann, 1984). We analyzed the first 10 calls that were not distorted by movement or the bird's position in the cage. Distance calls were digitized using Audiomedia digitizing hardware and software on a Macintosh IICI (Apple Computer, Inc.). We used a sampling rate of 44.1 kHz with 16 bit resolution. We used this sampling rate when we made spectrograms. To give better frequency resolution at low frequencies, all calls were desampled to 20 kHz and 12 bits for the analyses outlined below. This causes the spectrogram to extend over a smaller range of frequency and thereby show each band in greater detail.

### *Acoustic Analysis*

All analyses were performed using a commercial software package called Signalyze 2.47 (Keller 1992) that employs Fast Fourier Transform (FFT) to perform spectral analyses. The wild male's distance call

consists of a stack of harmonics with an initial frequency modulated (FM) upsweep, followed by a period in which the bands have little FM. In the second half of the call, the bands rapidly descend. (Zann, 1984, 1985). The part of the call in which FM is low is called the tonal element. The portion of the call with rapidly descending FM is called the noise element. The wild female's call closely resembles the tonal element of the wild male's call. The wild female's call does not contain a noise element (see Fig. 1).

We measured the same acoustic features that Zann (1984, 1985) used to analyze the distance calls of wild finches. The measures were as follows:

a) *Frequency of Maximum Amplitude (FMA)*: The frequency component of a call that, on average, had the greatest amplitude. This was measured by having Signalyze compute an average spectrum using a 512 point FFT with an effective resolution of 40 Hz. The average spectrum provides a measure of the average relative amplitude of the frequency components of a signal. We measured the amplitude of each peak by placing a cursor on the peak. The peak with the greatest amplitude was the FMA.

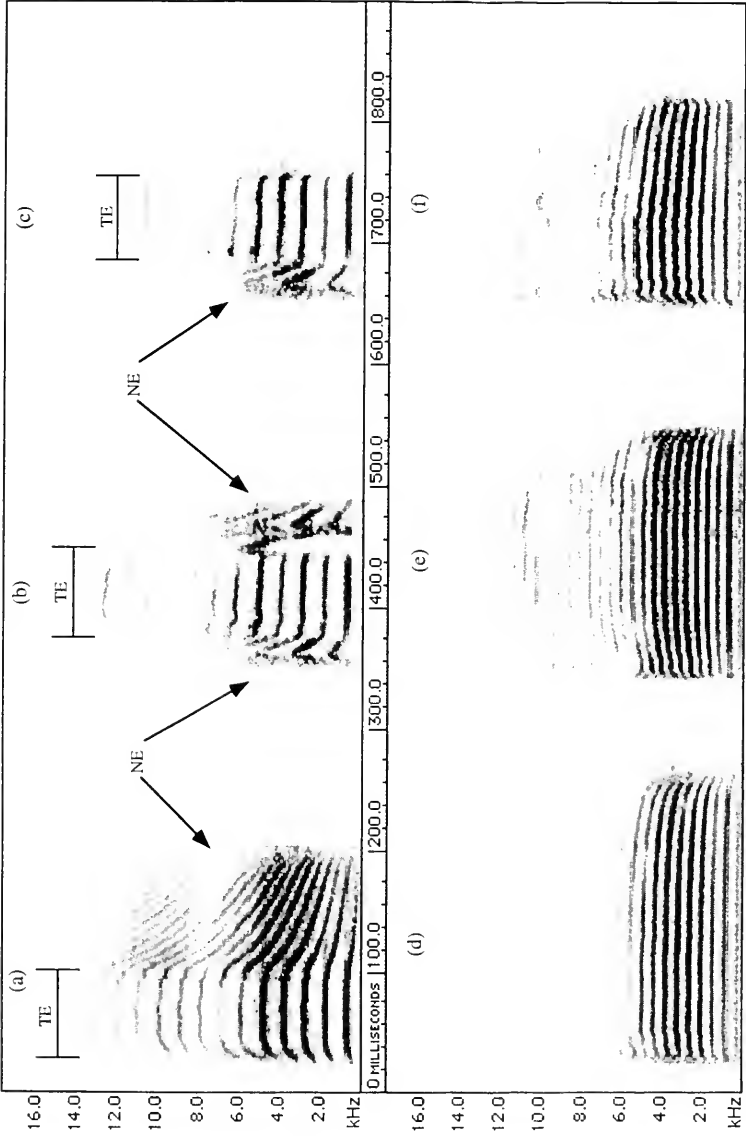
b) *Call Duration*: The duration of a call measured on an amplitude by time plot. The duration was measured and automatically calculated by highlighting the call with a cursor. The effective temporal resolution was 5 ms.

c) *Tonal Element Duration*: The duration of the tonal element was measured on a spectrogram. The tonal element is easy to discern on a spectrogram because its FM qualities are distinct from those of the noise element. Duration was measured using the technique described above. The spectrogram was made using a 512 point FFT, with an effective resolution of 40 Hz. In our population, only males produced calls which do not consist exclusively of an unmodulated tonal element.

d) *Fundamental Frequency ( $F_0$ )*: The lowest band of energy present in a call. This was determined by finding the lowest peak in a sound spectrum that could be divided evenly into the higher peaks. The spectrum was taken in the middle of a call using a 1024 point FFT. The effective resolution of the spectrum was 20 Hz.

e) *Location of the Noise Element*: Whether the noise element was located before, after, or both before and after the tonal element. This was determined by viewing a spectrogram of a call. The spectrogram was made using a 256 point FFT with an effective resolution of 80 Hz. Only males produce calls with noise elements. Okanoya et al. refer to the noise element as the auxiliary element and Simpson and Vicario refer to it as fast frequency modulation.





**Figure 1.** Spectrograms of the distance calls of three different males (a)-(c) and three different females (d)-(f). Note that each male has a noise element (NE) in a different location with respect to the tonal element (TE). Only male (a) has a distance call similar to that of wild zebra finches. These spectrograms were produced with SoundEdit Pro (Macromind-Paracomp, Inc.)

Okanoya et al. (1993) and Simpson and Vicario (1990) used similar digital techniques to analyze distance calls. Zann used a Kay Spectrum Analyzer to analyze the calls he recorded. To insure that any differences we found between distance calls of domesticated and wild finches did not result from different analytic techniques, we analyzed a number of distance calls using both FFT and a Kay Spectrum Analyzer similar to the one that Zann used. The results were similar. Measures of FMA differed, on average, by 26 Hz and measures of  $F_0$  differed, on average, by 22 Hz. Our measurements of  $F_0$  by FFT were always lower than measures of  $F_0$  on the Kay.

### *Statistical Analyses*

Zann (1984) provided means and standard deviations for call duration, tonal element duration, FMA, and  $F_0$  of wild male and female zebra finches. For domesticated finches, Okanoya et al. analyzed the same acoustic features as Zann, and Simpson and Vicario analyzed call duration,  $F_0$ , and gave some information about noise element location. Simpson and Vicario did not provide precise information about the standard deviation of each acoustic feature. Okanoya et al. measured only one call per bird.

To assess the degree to which distance calls have changed during domestication, we compared Okanoya et al.'s, Simpson and Vicario's, and our findings on domesticated birds to Zann's research on wild finches. We computed 95% confidence intervals for each acoustic feature that Zann measured using the method described by Jaccard and Becker (1990) for determining confidence intervals when the population value of the standard error of the mean is unknown. If the domesticated finches' mean call duration, tonal element duration, FMA, or  $F_0$  fell outside the 95% confidence interval for that feature, we considered the difference to be statistically significant. We used two-tailed t-tests to determine whether there were any sex differences in note duration, FMA, and  $F_0$  in our population. O'Brien's test was used to determine whether variances across groups were unequal. If there was a significant difference in variance across groups we used an unequal variance t-test.

Finally, like Zann (1984), we assessed the degree to which individual's calls were stereotyped by computing the coefficient of variation (standard deviation divided by the mean) for each bird on each acoustic feature. Neither Okanoya et al. nor Simpson and Vicario performed this measure. All statistical analyses were performed using JMP 2.0 (SAS Institute 1989).

## RESULTS

### *Call Duration*

In general, domesticated zebra finches produce distance calls that are longer than the calls of their wild counterparts (Table 1). Only one domesticated population, Okanoya et al.'s JNR females, produced calls that were approximately the same duration as those of wild females. Zann found that wild females produced longer distance calls than wild males. This was also true in three of the four domesticated populations. Female domesticated finches in Okanoya et al.'s ANR finches, Simpson and Vicario, and our population ( $t(255) = 11.9$ ,  $p < .0001$ ) produced distance calls that were significantly longer than those produced by males. The magnitude of the sex difference was approximately the same across the wild population and the three domesticated populations. Only Okanoya et al.'s JNR finches did not exhibit a sex difference in call duration.

### *Fundamental Frequency ( $F_0$ )*

Domesticated finches produce distance calls that, on average, have lower  $F_0$  than distance calls produced by wild finches (Table 2). This change is consistent with the fact that domesticated zebra finches tend to be larger than their wild counterparts (Sossinka, 1982; Carr & Zann, 1986). Zann found that wild females produce calls with lower  $F_0$  than wild males. Domesticated females also produced calls with lower  $F_0$  in three of four domesticated populations. In our population the difference was significant at  $p < .0001$  ( $t(255) = 13.8$ ). However, the difference in the  $F_0$  of distance calls produced by males and females is smaller in domesticated populations than it is in wild populations.

### *Frequency of Maximum Amplitude (FMA)*

In two of three domesticated populations in which FMA was measured, domesticated finches produced distance calls with higher FMA than wild finches. In addition, there were no sex-differences in FMA (Table 3). Zann found that wild males produce distance calls with significantly higher FMA than wild females. However, it is not clear to what extent the lack of sexual dimorphism in FMA among domesticated finches actually differs from Zann's findings on wild finches. First, wild finches from one of the two colonies Zann examined did not exhibit a sex difference in FMA. Second, the sex-difference in FMA in Okanoya et al.'s colonies is at least as large as the difference that Zann found.

**Table 1. The average ( $\pm$  SD) call duration (ms) of wild and domestic zebra finches, \* indicates that the value for domestic finches exceeded the 95% confidence limits for the wild population (same sex)**

Population Type	Study	Males	Females
Wild	Zann	140 $\pm$ 20	190 $\pm$ 30
Domestic	Blaich et al.	159 $\pm$ 38*	218 $\pm$ 41*
	Okanoya et al. (ANR)	188 $\pm$ 39*	242 $\pm$ 48*
	Okanoya et al. (JNR)	195 $\pm$ 54*	188 $\pm$ 61
	Simpson and Vicario	178*	268*

**Table 2. The average ( $\pm$  SD)  $F_0$  (Hz) of wild and domestic zebra finches, \* indicates that the value for domestic finches exceeded the 95% confidence limits for the wild population (same sex)**

Population Type	Study	Males	Females
Wild	Zann	1110 $\pm$ 210	620 $\pm$ 65
Domestic	Blaich et al.	892 $\pm$ 234*	575 $\pm$ 41*
	Okanoya et al. (ANR)	700 $\pm$ 206*	581 $\pm$ 56*
	Okanoya et al. (JNR)	969 $\pm$ 389*	540 $\pm$ 55*
	Simpson and Vicario	804*	568*

Okanoya et al. probably did not find this difference to be significant because they found more variability, and because they used a more conservative statistical test. Finally, it should be noted that the upward shift in FMA among domesticated finches may not reflect a change in the resonant quality of the domesticated zebra finches vocal tract. Rather, such changes may simply result from the alteration in the domesticated finch's  $F_0$  that we noted in the previous section. (See Nowicki (1987) for a discussion of vocal tract resonance in oscines.)

**Table 3. The average ( $\pm$  SD) FMA (Hz) of wild and domestic zebra finches, \* indicates that the value for domestic finches exceeded the 95 % confidence limits for the wild population (same sex)**

Population Type	Study	Males	Females
Wild	Zann	3750 $\pm$ 560	3540 $\pm$ 330
Domestic	Blaich et al.	4102 $\pm$ 741*	3983 $\pm$ 672*
	Okanoya et al. (ANR)	3833 $\pm$ 403	3608 $\pm$ 325
	Okanoya et al. (JNR)	4262 $\pm$ 806*	3700 $\pm$ 731*

**Table 4. The average ( $\pm$  SD) tonal element duration (ms) of wild and domestic zebra finches, \* indicates that the value for domestic finches exceeded the 95 % confidence limits for the wild population (same sex)**

Population Type	Study	Males
Wild	Zann	45 $\pm$ 20
Domestic	Blaich et al.	109 $\pm$ 42*
	Okanoya et al. (ANR)	147 $\pm$ 48*
	Okanoya et al. (JNR)	182 $\pm$ 75*

*Noise Elements and Frequency Modulation*

Domesticated males produce distance calls in which the noise element is shorter than the wild males' noise element. This is consistent with our finding that tonal element duration (the remaining portion of the male's call) is much longer in calls produced by domesticated males (Table 4). Zann (1985) reported that the duration of the tonal element is normally 1/4–1/2 of the call duration (See Fig. 1, bird (a)). Most domesticated males produce calls in which tonal element duration is about 1/2–2/3 of the call duration (see Fig. 1, birds (b) and (c)).

Zann (1984) reported that 99% of wild males produce distance calls in which the tonal element is followed by a noise element. This pattern was far less frequent among domesticated males. Indeed, there is little

consistency in the location of the noise element across domesticated populations. Instead, the noise element may be found before the tonal element, before and after the tonal element, in the middle of the tonal element, or entirely absent. (For examples see Fig. 1, birds (a)-(c).) In three of the domesticated populations (Okanoya et. al. [ANR], 1993; Simpson & Vicario, 1990) the noise element was most often located at the beginning of a call. In our population at least, individual males placed their noise elements in the same location every time they called. This is consistent with the pattern exhibited by wild males.

The frequency modulation of domesticated males' noise elements were also quite different from those of wild males. A number of our birds displayed noise elements with sharply ascending and then descending FM. On a spectrogram these noise elements resembled inverted "V"s (see Fig. 1, birds (b) and (c)). In wild finches, the FM of the noise element typically descends only, and the change in frequency is more gradual (see Zann, 1984, 1985). Only one of our domesticated males produced a distance call whose noise element resembled that of a wild male (Fig. 1, bird a). Generally, domesticated males produced noise elements in which the rapidly descending FM portion appeared to be cut off relative to the noise elements of wild males.

Otherwise, the FM of both the male's tonal element and of the entire female's call appeared to be similar to the FM of calls produced by wild finches. Spectrograms of the distance calls of domesticated females (see Fig. 1, birds (d)-(f) appear to be virtually identical to those Zann (1984, 1985) published of wild females.

### *Call Stereotypy*

One area in which the calls of domesticated males did not differ from those of wild males was in the degree of call stereotypy. Domesticated males in our population showed levels of within-subject variability on call duration, tonal element duration, and  $F_0$  comparable to those of wild finches (see Table 5). However, there was far more within-bird variability in FMA. Thus, while the spectral characteristics of distance calls produced by domesticated males in our population were quite different from those of wild males, the degree of call stereotypy was not. Distance calls of domesticated and wild females showed comparably low levels of within-bird variability on  $F_0$ . However, domesticated females had higher coefficients of variation on call duration and FMA (Table 5).

**Table 5. Median coefficient of variation for call duration, tonal element duration, FMA, and  $F_0$  of domestic male, wild male, domestic female, and wild female zebra finches. The median coefficients of variation for wild birds were calculated from Zann's (1984) results.**

	Domestic males	Wild males	Domestic females	Wild females
Call duration	.036	.038	.104	.046
Tonal element duration	.063	.065	n/a	n/a
FMA	.108	.015	.124	.019
$F_0$	.022	.015	.016	.019

## DISCUSSION

According to Lickliter and Ness (1990) domestication, "...refers to the process by which organisms change in terms of morphology, physiology, or behavior as a result of the human control of their breeding, feeding, and care (p. 211)" (See also Hale, 1969; Miller, 1977). It is evident that the different forms of human control outlined by Lickliter and Ness have changed the distance calls that domesticated zebra finches produce. In general domesticated males and females produce calls that have longer duration, lower  $F_0$ , and higher FMA. However, it should also be noted that these changes are quite subtle. In some cases the differences between some domesticated and wild populations were smaller than the differences among domesticated populations.

The males' noise element is the most obvious acoustic feature that has changed as a result of domestication. The frequency modulation of noise elements produced by domesticated males often differed dramatically from those produced by wild males. This change should not be surprising. There is clear evidence that young males model their noise element on those that they hear during development (Zann, 1985; 1990). Given this degree of developmental plasticity, cultural changes alone may account to a large extent for the different noise elements that domesticated and wild males incorporate into their distance calls. Yet, as obvious as the change in the structure of the noise element is, it should be noted that the role of this acoustic feature in the function of

the distance call is not clear. Thus, changes that have occurred during domestication in the structure of the noise element may have little or no effect on the function of the call.

We believe that the remaining changes in the distance call that have occurred across domesticated populations, as subtle as they are, are not due solely to changes in the calls that domesticated zebra finches hear when they develop. With the exception of the noise element, the development of most features of the distance call do not change when young finches are reared in an abnormal acoustic environment. Zann (1985) cross-fostered zebra finches using Bengalese finches as parents. Although the noise element of foster-reared males developed abnormally, there was no difference in the FMA,  $F_0$ , and call duration of foster reared and normally reared males. Foster-reared females had slightly higher  $F_0$  than normally reared finches (by 30 Hz), but their calls did not differ in FMA, call duration, or frequency modulation.

Some authors have argued that male and female zebra finches differ in the degree to which the development of their distance calls is altered by experience. For example, Simpson and Vicario (1990) stated that three features of the male's distance call are learned from external models: high  $F_0$ , call duration, and the noise element. They also state that the development of distance calls among females is not altered by external models. We believe that the evidence supports a more subtle interpretation. Although the development of the males' noise element is clearly altered by experience, it is not clear how to relate this finding to call development in females since females don't use noise elements in their calls. Furthermore, Zann's (1985) findings on the effects of cross-fostering on the remaining acoustic features of distance calls don't point to a large sex difference in developmental malleability.

Okanoya et al. (1993) argue that sexual dimorphism in the acoustic structure of the zebra finches' distance call is gradually disappearing during domestication. Our findings are generally consistent with their claim. First, the reduction in the size of the male's noise element, and consequent enlargement of the their tonal element, has reduced the sex difference in the frequency modulation of the distance call. Second, the difference in  $F_0$  is smaller among domesticated finches than it is among wild finches. The difference in FMA also appears to have decreased. However, this change should be treated with some caution since Zann (1984) did not find a consistent sex-difference in FMA among wild populations that he studied. Thus, it is not clear to what degree a consistent sex difference in FMA exists in wild zebra finches.

Zann (1984) hypothesized that the primary function of the distance call in the wild is to allow breeding pairs to maintain contact in large



flocks. Despite changes that have occurred in the structure of the distance call during domestication, we believe that there may be sufficient inter-individual variability and intra-individual stereotypy to allow this function to be retained in domesticated birds. Dooling et al. (1992) have shown that domesticated finches can distinguish distance calls of different individuals. However, their paradigm required zebra finches to differentiate four different calls from four different birds. The task of distinguishing the distance calls of a mate from those of other finches in a large flock is probably more difficult. Thus, it remains to be experimentally demonstrated that domesticated zebra finches can use distance calls to recognize their mates.

A number of researchers have used domesticated zebra finches as models to investigate the physiological and acoustical basis of call production and perception (Dooling et al., 1992; Okanoya & Dooling, 1987, 1991 a, 1991b; Okanoya et al., 1993; Simpson & Vicario, 1990). Despite this fact, there is no research on the functional significance of the various calls that zebra finches produce. We believe that such work will be important not only for a greater understanding of the natural history of zebra finches, but also to understand how the production and perceptual capacities that have been so carefully studied play a role in the behavior of this species.

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# ANAGENETIC THEORY IN COMPARATIVE PSYCHOLOGY

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**ABSTRACT:** This paper is a response to Campbell and Hodos' continuing critiques of the field of comparative psychology. Their opinion to the contrary, I show that anagenesis is still a useful concept to evolution scientists and that anagenetic analysis provides a viable and fruitful approach to theory development in comparative psychology. Anagenesis suggests improvement with evolution and the idea of complexity as an indicator of evolutionary progress is discussed. Finally, the paper discusses the utility of a modified form of the *Scala naturae*, namely the concept of integrative levels by showing how T. C. Schneirla has used this idea as the foundation of his significant theoretical contributions to comparative psychology.

## INTRODUCTION

In their widely discussed critique of comparative psychology, Hodos and Campbell (1969) indicted the field on the grounds that it was not based on a valid theoretical orientation. They asserted that comparative psychologists misunderstood evolutionary theory, citing its long history of capricious comparisons, i.e., comparisons of behavioral differences among animals that do not represent "true" evolutionary lineages. Needless to say, their paper generated a substantial response (e.g., Gottlieb, 1976, 1984; Tobach & Adler, 1974). The argument was made that Hodos and Campbell were wrong, that comparative psychology was indeed guided by theory, evolutionary theory, and that the *Scala naturae*, while dated and outmoded, still offered some important guidance in making generalizations about evolution and behavior. Their critical commentary has continued to the present (Campbell, 1976;

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Campbell & Hodos, 1991; Hodos & Campbell, 1990).

I am reminded of what the late Harry Helson told us as graduate students: that as editor of the *Journal of Experimental Psychology* he did not enter debates such as this because he believed they did not contribute to scientific advance. Indeed, the present debate has been characterized as being "acrimonious" (Gottlieb, 1984). I do believe, however, that continuing this dialogue in a constructive manner can be useful in helping us redefine and refine our formulation of the significant questions that need to be asked about behavior and evolution. The most recent focus of this debate is the continued use within comparative psychology of "anagenetic analysis" (Campbell & Hodos, 1991; Hodos & Campbell, 1990). A related issue is the utility of an hierarchical perspective.

The position taken in this paper agrees with Gottlieb's (1984) contribution to this discussion: "There is a theory in comparative psychology, and that theory is a hierarchical classification of adaptive behavior by grade [i.e., anagenetic analysis], independent of cladistic (i.e., genetic) relationship" (p. 454); and, "Anagenesis is of course not the only theory in comparative psychology, but it has been a major one since at least as early as the 19th century" (p. 449).

Some comparative psychologists have proposed the concept of anagenesis be used as an alternative formulation of the evolutionary scale (e.g., Gottlieb, 1984; Yarczower, 1984; Yarczower & Hazlett, 1977; Yarczower & Yarczower, 1979). Campbell and Hodos (1991) find fault with anagenesis because of a failure among evolution scientists to agree on its definition. Nevertheless, while there has been disagreement as to whether anagenetic changes occur within grades or clades (Gottlieb, 1984), whether they apply to changes in parallel or convergent evolutionary processes (Yarczower & Hazlett, 1977), or whether such changes reflect our own anthropocentric views of the universe (Huxley, 1942, 1957), the concept still plays a role in discussions of evolution (e.g., Devillers & Chaline, 1993; Futuyma, 1987; Gould & Eldredge, 1993; Panchen, 1992). Current usage appears to uniformly refer to progressive evolutionary change (Davey, 1989; Panchen, 1992, 1993; Scott-Ram, 1990).

In expressing their concerns about anagenesis, Hodos and Campbell (1990) join a long list of scientists in pointing out the difficulty of satisfactorily defining evolutionary progress, the ongoing discussion of which is as old as Darwin's ideas themselves (Richards, 1992). Many, including this author, see merit in identifying evolutionary progress with increasing complexity and level of organization (e.g., Bonner, 1988; Dobzhansky, 1955; Lewin, 1992; Pantin, 1951; Stebbins, 1969; Wesson,

1991). An increasingly common approach to complexity equates it with improved information processing associated with nervous system evolution and advance (Jerison, 1994; Lewin, 1992).

While at one time it could be said that the concept of complexity had been neither adequately nor accurately treated in biology (Pringle, 1951), this is no longer the case (Wicken, 1984). In the first of a series of papers, Saunders and Ho (1976, 1981, 1984) presented an argument for the use of the dimension of "complexity" as a measure of progress in evolution, contending that it is:

*...the fundamental parameter in evolution. An obvious advantage is that there is no difficulty in defining it; von Neumann (1966) defined complexity of an automaton to be the number of components it contains and there does not appear to have been any serious disagreement with this choice, although for biological systems a better measure is the number of different types of components.... Increase in complexity is also comparatively easy to observe, so we have a practicable partial ordering of species.... [I]ncrease in organization... is a secondary effect and comes about simply because the more complex a system is, the more organization it needs to survive...." (p. 377, italics added).... "[I]n our view there are two separate laws of evolution, survival of the fittest and increase in complexity.... (p. 383, italics added)*

Indeed, there are now even "sciences of complexity" including ecology, economics, cognitive psychology and artificial intelligence (Lewin, 1992; Wesson, 1991).

This concept of progress in evolution is consistent with the important theoretical concept of integrative levels (Feibleman, 1954; Needham, 1943; Novikoff, 1945; Redfield, 1942) that Aronson (1981, 1984) has proposed be used as the basis for comparison in comparative psychology. The levels concept, he said:

*... is a view of the universe as a family of hierarchies in which natural phenomena exist in levels of increasing organization and complexity. Associated with this concept is the important corollary that these successions of levels are the products of evolution. Herein lies the parallel with anagenesis. (1984, p. 66)*

Again, Hodos and Campbell (1990) have rejected this argument, seeing no essential differences between the levels concept and anagenesis.

In contemporary usage, anagenetic analysis implies "improvement" with evolution (Panchen, 1992), hence the connection to the *Scala naturae*, which is alleged to have no place in contemporary science (Campbell & Hodos, 1991; Hodos & Campbell, 1969, 1990), although there is not universal agreement about this. Gould (1976), for example, says:

*...it seems as though comparative neurologists remain rooted to Lamarck's scala naturae - for they persist in studying a fish, a reptile, an insectivore, a tree shrew, a monkey, and a man and in drawing from such comparisons a set of conclusions about vertebrate evolution... Paleontologists then seem to*

assert that because the series does not reflect true descent, it cannot designate anything of value. I propose ... that *this procedure, nonetheless, is both valid and valuable; and ... that it reflects an evolutionary concept of undoubted respectability*, despite its inevitably subjective basis (p. 115, italics added.)

Such reasoning is likely responsible for the persistence of comparisons among such "typical" animals as fish, frogs, turtles, alligators, pigeons, rats, cats, dogs, monkeys and humans in current textbooks in many of the sciences -- comparative anatomy, comparative physiology, comparative endocrinology, etc. (Burghardt & Gittleman, 1990). It is of interest to note that evolution scientists are not of one mind on the respectability of the idea of "progress." Gould's (1994) strong position on evolutionary progress is not shared by all evolution scientists and may reflect an ideology (Lewin, 1992). Indeed, according to Preuss (1995), the idea that brain evolution reflects a progressive trend towards improved information processing is a traditional way of thinking in neuroscience and psychology:

That is to say, the pattern of brain evolution has been likened to a unitary scale or ladder rather than to a branching tree (p. 1230)

Hodos and Campbell (1969) began this debate by rejecting comparative psychology's use of some form of the evolutionary scale because it does not in any way represent a true historical lineage. Using the the work of Bitterman (1965 a,b) as an illustration, they have called such comparisons capricious (p.349) and absurd (1990, p. 1). This, however, loses sight of the fruitfulness and success of this approach as the following statement by Tobach (1976) underscores:

Depending upon the question being asked, and the level of organization under investigation, the comparison [between mouse, rat, cat and monkey] is extremely fruitful... [particularly] in view of the fact that at this stage of knowledge there is no one criterion that has proved to be the most significant in determining the species to be compared. It has been said that if the tests for toxicity of thalidomide had been carried out on sea urchin eggs instead of adult mammals, the drug would not have been passed on for general use. The choice of question and animal to be investigated depends on many factors other than nearness of evolutionary relationship. (pp. 196-197)

A similar argument has been made by biologists as well. Wood (1972), for example, argued that, despite their distant evolutionary relationships, toxicity tests on rodents can provide quite valid indications of human reactions. Thus, it seems clear that such comparisons are not absurd but they can be quite useful.

Davey (1989) recently suggested that anagenetic analysis by grade provides a solution to the criticisms of Hodos and Campbell (1969) about "capricious" comparisons. Such analysis requires the elucidation of the (subjective) criteria used to identify different grades. His preference is to define grades as ascending series of improvements

which he illustrates with two much cited examples. The first approaches the definition of higher grades from a physiological perspective in which species are ranked with respect to the relationship between brain and body size (Jerison, 1973, 1994). This produces an objective measure, the encephalization quotient, "a true dimension based upon objectively measured structural attributes" (Plotkin, 1983, p. 128). Olson (1976) showed the relationship of this progressive encephalization quotient to represent a greater capacity to process information. A similar argument was presented by Killackey (1990) in his discussion of neocortical expansion and improved information processing which follow phylogenetic lines. Improved information processing was earlier recognized by Pantin (1951) to be a crucial indicator of evolutionary advance.

Davey's (1989) second example is Hölldobler and Wilson's (1983) description of progressively improved nest construction by some formicine ants in which higher grades are represented by improved adaptational strategies. Other examples include Razran's (1971) formulation of a hierarchical arrangement of learning capacities through eleven levels from "habituation and sensitization" to "thinking" and the discussion of "learning sets" in which evolutionary (phylogenetic) trends have been identified (e.g., Warren, 1965).

Campbell and Hodos (1991) cite Demarest (1983) who portrays the anagenetic analysis of learning as a failure. However, Demarest offers no evidence for this point beyond merely stating that since learning does not leave fossils, we can not discover its evolutionary course. It has, however, been long recognized that it is the organism rather than its behavior which evolves (e.g., Tierney, 1986), the course of evolution endowing organisms with increasingly complex behavioral potentials (Kuo, 1967).

This useful approach to taxonomy is labeled *pheneticism* by Harvey and Pagel (1991). In pheneticism, taxonomic position is decided by phenotypic similarity rather than by phylogeny. One successful theoretical formulation from this perspective is that developed by T. C. Schneirla (Aronson, Tobach, Rosenblatt & Lehrman, 1972), whose description of "behavioral levels" represents a somewhat less subjective approach to defining successive grades as do the foregoing examples. Gottlieb (1984, 1985) has referred to this theoretical approach as behavioral analysis by grades, in which each new behavioral level is considered a new grade. In principle, taxonomy has always been somewhat subjective and arbitrary (Barnes, 1984; Brooks, 1983; Goldsmith, 1991; Gould, 1982; Harvey & Pagel, 1991; Miles & Dunham, 1993; Simpson, 1961; Sokal, 1974) so many orderly

arrangements are possible, including that proposed by Schneirla. It is of some significance to note that while Eldredge (in press) indicates that the concept of "grade" is little used among contemporary evolutionary biologists, he identifies Schneirla's use of the concept as an important explanatory tool for comparative psychology.

The levels concept, which serves as the cornerstone of Schneirla's theory (1949, 1953), suggests the ranking of animals with respect to their degree of behavioral plasticity. Animals less behaviorally plastic function at lower behavioral levels at which biological processes are of great significance; more behaviorally plastic organisms function at higher behavioral levels at which psychological processes (e.g., mediation) direct the course of behavioral development. Increased behavioral plasticity is a result of increasing nervous system advance, complexity, and organization. Tobach and Schneirla (1968) proposed a hierarchy of behavioral levels: taxis, biotaxis, biosocial, psychotaxis and psychosocial. The utility of this idea was recognized as early as 1900 by Hachet-Souplet (Small, 1901) and has served as one of the themes of all of the T. C. Schneirla Conferences (Greenberg & Tobach, 1984, 1987, 1988, 1991, in press; Hood, Greenberg, & Tobach, in press).

The hierarchy proposed by Tobach and Schneirla (1968) should not be considered complete; it is rather an initial attempt at bringing order to behavioral comparisons. For example, as originally proposed, primates were ranked at the highest behavioral level, the psychosocial. However, combining all the primates into a single level ignores the enormous diversity and richness of primate behavior. For example, it is now widely believed that apes, and especially chimpanzees, are capable of true linguistic processes (Savage-Rumbaugh, Murphy, Sevcik, Brakke, Williams & Rumbaugh, 1993), though at a level substantially less complex than in *Homo sapiens*. This suggests grade differences between language and non-language using primates and *Homo sapiens*. I propose a refinement of the originally proposed single psychosocial level into three: Psychosocial 1 (includes all non-language using primates), Psychosocial 2 (language using apes), and Psychosocial 3 (*Homo sapiens*). While she alluded to this type of analysis in a recent discussion of animal cognition, Tobach (1987) went no further than drawing attention to the utility of a levels orientation in thinking about language processes. This approach is useful, too, in comparing learning capacities among the primates in an evolutionary framework (e.g., Rumbaugh & Pate, 1984).

It should be emphasized that the criticisms of Hodos and Campbell are not uniformly shared by all evolution scientists. No one can claim to have the final answer in this debate, including the present author. It is



my hope that Hodos and Campbell would agree with this point. A constructive attitude about this is reflected in Ho and Saunder's (1984) admonition that:

It must not be supposed however, that there is anything approaching the 'consensus' which is often claimed for the neo-Darwinian synthesis. Pluralism is a predominant feature of the [*still*] emerging paradigm of evolution. Not only is there a genuine (and in our view, healthy) diversity of opinion and emphasis, but evolution is a complex phenomenon and it is to be expected that different kinds of explanations will be appropriate to different aspects. Thus, pluralism ought in principle to be a permanent feature of evolutionary studies. (p. 5)

Along these same lines, Gottlieb (1984) has said:

Although one cannot disagree with the factual basis of Hodos and Campbell's claim about evolutionary lineages, one can question whether their understanding of the terms *evolutionary* and *phyletic* is rather too narrow, not only for comparative psychology but for evolutionary biology as well... (p. 448).

This debate began in 1969 with the charge by Hodos and Campbell that there was no theory in comparative psychology. In response I have tried to show that Schneirla began the important task of building a comprehensive theory of behavior; his students and colleagues have undertaken the empirical work which has led and still is leading to the discovery of principles and laws upon which that theory rests. While it was unfortunate that Schneirla died when his theory was still incomplete, his ideas continue to influence researchers in comparative and developmental psychology. In this context I find merit in Harvey and Pagel's (1991) defense of pragmatism in the search for truth, especially when intellectually challenging ideas are involved. I have tried to show, as have others before me, that this debate can be useful and that denying the existence of valid theory in comparative psychology is shortsighted.

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## THE DEVELOPMENT AND INTEGRATION OF BEHAVIOUR: A TRIBUTE TO ROBERT HINDE

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**The development and integration of behaviour: Essays in honour of Robert Hinde**, edited by Patrick Bateson, Cambridge: Cambridge University Press, 1991.

*The Development and Integration of Behaviour* is a very well-edited commemorative volume honouring almost half a century of Robert Hinde's scientific work. The distinguished scholars, including a Nobel laureate, who have contributed to the book represent a wide range of backgrounds: ethology, ecology, psychology, psychiatry, and neuroscience. The multidisciplinary nature of the book exemplifies the need for cooperation among scholars from many different disciplines in order to further the study of the "development and integration of behaviour." This, appropriately, is the title of the book, and also the name of Hinde's research unit at Cambridge University. It is exciting and stimulating to see scientists with different backgrounds, and therefore greater knowledge and expertise than any individual alone can provide, unite to attack these scientific problems.

This book is important because the contributors provide invaluable information for all those interested in the biology of behaviour; it is unique because the person honoured provides stimulating and cleverly-argued commentaries on these contributions. Therefore, it is also an interesting example of Hinde's definition of "process."

Personally, I would like to take this opportunity to acknowledge my

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own indebtedness to Robert Hinde - for his teaching and his personal generosity. I am lucky to have had the opportunity to experience and learn from Hinde's wise counsel and rigorous, seminal thinking during his visits to my Department and his participation in scientific meetings on the brain and aggression organised by my research team. He was one of the main contributors to the Seville Statement on Violence, the result of an interdisciplinary meeting of scholars from all continents convened by me under the auspice of UNESCO. Together with Jo Groebel, we co-edited a book, *Essays on Violence* (1987), which may be regarded as the first volume of Hinde's trilogy on violence, war and co-operation. The other two books are *Aggression and War* (1989) and *Cooperation and Prosocial Behaviour* (1991).

Because of my personal involvement with Hinde, I shall not limit myself to a standard book review, but rather take this opportunity to stress some of his main ideas, which are also included in the present volume. This seems most appropriate because, to use the words of Hinde's former student, Jane Goodall, whose field studies with chimps in Tanzania are known the world over, he "will surely take his place as one of the giants of our times" (p. 470).

One of Hinde's most important contributions to science is his continued attempt to develop coherent links between theory and data. His penetrating new insights have given rise to conceptual clarification of behavioral processes and developmental psychobiology. He has also provided a change in the framework of inquiry which is most illuminating. It may be best to treat the empirical and conceptual divisions concerning patterns of behaviour as heuristics leading to a deeper understanding not truths in themselves. An important guide for research is to adopt a balance between analysis and synthesis.

The illustration on the cover of *The Development and Integration of Behaviour* depicts the species that Hinde has studied most extensively: a bird, representing his earlier ornithological work on song-learning and filial imprinting; a monkey, indicating his research on the development of social behaviour; and two children, representing his most recent work on mother-infant relationships that extends his analysis of social structure to humans.

The sections of the book clearly reflect the themes of Hinde's scientific work: behavioural development; behavioural neuroendocrinology; social behaviour, and its development in human and nonhuman primates; aggression and war. As well, there is an introduction by the editor and a final section with personal memoirs - by Niko Tinbergen and Jane Goodall. Hinde's very-appropriate commentaries conclude each section. A summary of Hinde's research career and a short history

of the Subdepartment of Animal Behaviour at Madingley are included in appendices.

The book begins with two notable ethological examples of behavioural development in birds: imprinting and song-learning. Patrick Bateson discusses imprinting, and illustrates how the complexities of development might be made more tractable by uncovering principles that make sense of that complexity. One of his conclusions is that the traditional nature-nurture dichotomy is useless. Peter Marler discusses the interplay between the developing bird and its environment, using as an example song-learning in different species. He emphasises the importance of understanding the rules that underlie developmental processes and the crucial influence of genetic factors in generating differences between species.

The next section is dedicated to neural and endocrine aspects of behaviour. John Fentress, in an optimistic attempt to reassemble the integrated organism, takes a neuroethological approach, stressing the importance of a bi-directional perspective in the interconnection between behavioural and neural analysis. His general point is elaborated further in the following chapters. Gabriel Horn uses imprinting in chicks to illustrate how the interconnections between different levels of analysis are made in practice. Reporting work with both birds and mammals, John Hutchison links the behavioural analysis of courtship with the biochemical techniques of neuroendocrinology; i.e. whether or not a behavior pattern is expressed depends on brain enzymes, which in turn depend on the animal's state, which in turn depends on environmental conditions. Richard Andrew comments on the various actions of testosterone on behaviour; for example, it makes animals less distractible perhaps by increasing attention span. Finally, by extending his intensive research in rodents to primates, Jan Rosenblatt attempts to find more general principles of the organisation of behaviour and demonstrates the value of a comparative approach to the study of maternal behaviour.

The section on social organization in non-human primates begins with Tim Clutton-Brock's comparative study of the mating system and its ramifications for other aspects of the biology of the species. He too stresses the influence of environmental conditions. In her chapter, Thelma Rowell suggests the importance of treating animals as individuals, instead of as universals, when analysing different levels of behaviour. Finally, using human examples, Michael Simpson offers a valuable insight concerning commitment in social behaviour.

The first three chapters of the section on the development of human behaviour are dedicated to the long-term effects of mother-child relationships. John Bowlby tries to integrate psychoanalytic and



ethological concepts; Joan Stevenson-Hinde defends a dynamic interplay between attachment and temperament, rejecting its traditional and unfortunate dichotomy; and Michael Rutter considers the negative long-term effects of maternal deprivation on adult behaviour. The last two chapters of this section, by Judy Dunn and Marian Radke-Varrow, respectively, demonstrate the valuable methodological contribution Hinde's ethological work with animals has made to research in child development.

Finally, David Hamburg, in the section on human aggression and warfare, hopes that the human capacity to adapt to new conditions may be enhanced if we know more about evolution. Violent behaviour may be controlled, if we can understand the conditions under which it is likely to be expressed (see also, Ramirez, 1994).

One of Hinde's continuing messages, endorsed in this book by old friends and students, is that "even though the move in every subject is towards greater specialisation and towards reducing large problems to smaller ones at lower levels of analysis, satisfying explanations are rarely going to come from one method or a single theoretical framework" (Bateson, Chapter 1, p.14). To achieve understanding scientists need to "cross and recross" - to use one of his typical expressions - the boundaries between different levels of analysis and disciplines. This means having a more problem-oriented focus, as Hinde does with his fertile, eclectic approach.

Since this review is for the *International Journal of Comparative Psychology*, it seems appropriate to acknowledge Hinde's immense contribution to the synthesis of ethology and comparative psychology, expressed in his now classic book *Animal Behaviour* (1966). Here he pointed out the continuities between seemingly diverse ideas, uniting them into a complex whole, with a wide range of mediating processes. Hinde stressed to his students the importance of a comparative approach to the study of behaviour, while never neglecting the study of species differences; the need to integrate data from different groups of animals; and the idea that advances in understanding animal behaviour may lead to questions that will eventually help us to understand ourselves. An interesting example of this last assertion is Simpson's imaginative insight on declaring commitment to a partner (Chapter 11). Hinde also made the important suggestion that research on animal behaviour should be approached separately from the four classical perspectives of ethology: causation, development, function and evolution; and that these approaches may be mutually beneficial. For example, functional considerations can help us answer developmental questions, and causal analysis can contribute to evolutionary studies.

Thanks to Hinde's penetrating new insights, the internecine strife and sterile controversy between ethology and comparative psychology has largely disappeared. Hinde (1982) himself admitted that "aggressive overtures are common on interdisciplinary boundaries, and I erred in that way myself. In the long run, of course, liaison must depend not on territorial invasion, as I implied, but a mutual welcome for those who cross no-man's-land" (1982, p. 16). One now may suggest, using Bateson's rather apt expression, that "Cinderella has finally arrived at the ball" (Chapter 2, p. 37).

To summarize, this book is proof that a liaison between different disciplines can take place, and in a fertile manner. Moreover, the utility of the ethological approach to the biological and social sciences is strongly supported. The very challenging and diverse contributions presented here are of great interest and importance for all students of the biology of behaviour.

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